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THE PHYLOGENETIC POSITION OF *ATRACTOCERUS* Palis.

By Edwin W. King[1, 2]

The genus *Atractocerus* was described in 1802 by Palisot de Beauvois, and at present contains approximately a dozen species, distributed throughout the tropical and subtropical regions of the world. The species have long been recognized by many workers as being a bizarre, unorthodox coleopterous type—Lacordaire, in 1857, expressed well the doubt that has existed concerning them when he wrote "Ces insectes ont plutôt les *facies* de certaines Nevropterès que des Coleoptères." But he does not elaborate, and a succession of workers (Paulian, Böving and Craighead, Sharp and Muir, Forbes, Woodworth, Redtenbacher, and Barber) have all placed the genus in the family Lymexylonidae, sometimes with some reservations. It is the purpose of the present paper to re-examine, with special reference to the wing venation and female genitalia, the relationships of this genus to those with which it has been most commonly associated: *Hylecoetus, Melittomma* (*Lymexylon*), and *Telegeusis.*

The genus *Atractocerus* (fig. 1) may be briefly characterized as follows: head round, eyes holoptic or nearly so; antennae fusiform; maxillary palpi with short flabellate processes, the galea and lacinia reduced to short stubs; labium with mentum and submentum elongate, extending between the bases of the maxillae so that the latter lie outside of the mouth cavity; prosternum with only a narrow strap of scleritization anterior to the coxal cavities, the remainder membranous; anterior trochantins large; tarsi pentamerous, elongate, and simple; elytra greatly

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reduced; hind wings not shortened by folding, their venation with no recurrents and only one crossvein; abdomen with seven visible ventral segments, eight dorsal; male genitalia with lateral lobes forming variously shaped antler-like processes; female genitalia with coxites large, valvifers reduced.

In the past the assumption has been made that *Atractocerus* was a bizarre relative of that group of genera which have made up the Lymexylonidae and Telegeusidae. Evidence in favor of this view is at best rather indecisive, and evidence contrary to it may have gone somewhat unappreciated. The hypothesis set up here is this: In the course of evolution from some megalopterous type the ancestors of the order Coleoptera lost certain veins of the hind wing, transformed the front wings into elytra, and acquired the power to fold the hind wings in the complex folding patterns common today among beetles. The hypothetically ancestral structures of both larva and adult assumed features which may be and have been deduced from existing forms. However, it is most unlikely that all these changes occurred simultaneously, or were ever all present at one time in a given species. If a form diverged early from the beetle line, before all the basic features of the Coleoptera had become established, one would expect of it three things: a) that it should retain some features of its pre-coleopterous ancestor not shared by other beetles; b) that it should have developed specializations of its own not shared by other beetles; and c) that it should develop certain features in parallel with other beetles when it is exposed to the same selection pressures as they. *Atractocerus* appears to be such a form.

The Hind Wing

Forbes (1922, '26), in his excellent papers on coleopterous venation and wing folding, notes the fact that the wing of *Atractocerus* lacks any transverse folding and that the venation is extremely simple. He regards both conditions as specialized from a more typical coleopterous wing. It seems possible that these facts may have a different explanation, and lead to a different conclusion.

One obviously must begin by working out as accurately as possible the homologies of the veins. The wing venation of *Atractocerus* sp. is shown in figure 2a; the enlarged base of the wing in figure 2b. Costa, Subcosta, and Radius present no particular problems. Costa lies in the wing margin and is distinguishable only at its base. Subcosta, as in other insects, articulates with the apex of the elongate first axillary sclerite (I). Radius, in the Coleoptera, is the first strong longitudinal vein, and the position, convexity, and basal articulation to the second axillary sclerite (II) all indicate that the vein here labeled R may safely be called Radius.

In the wings of insects in general, Media and Cubitus arise not directly from a primary basal sclerite but from the median plate (m), a sclerotized area distal to the axillaries. The median plate is divided by the base of the cubital furrow, which, when extended into the wing proper, marks with great consistency the separation between the anal and cubital veins. This fold can be traced without difficulty through the median plate in the wing of *Atractocerus,* and divides the plate into a proximal part (m) and a distal part (m′). However, the fold does not extend far into the wing membrane. Plate m′ in *Atractocerus* is in turn weakened and divided by a membranous area. The vein lying posterior to Radius extends to the base of the wing, and there unites with the anterior part of m′. It cannot, therefore, be the Radial sector, and must be either Media or Cubitus. If it is Cubitus then the next posterior vein, which arises from another part of m′, has three convex branches, and lies entirely anterior to the cubital furrow, must be the 1st Anal of Comstock and Needham. In that case one is forced to acknowledge a three-branched 1st Anal and the complete disappearance of Media. An hypothesis which more satisfactorily fits the facts is that the three-branched vein is Cu_1 + 1st A. In support of this interpretation, the following points may be noted. (1) Cubitus, as well as Media, often articulates with the median plate, as does this vein. (2) Cu_1 is strongly convex, and its branches, when they occur, are also convex. (3) In other Coleoptera (i.e. *Cupes,* fig. 3a, b) and also in at least a few Megaloptera (*Corydalis*), 1st A is associated at its base with the median plate, rather than with the third axillary as are the other anals. Its fusion basally with the base of Cubitus is not difficult to visualize. (4) 1st A is a convex vein; all three branches of the vein in question are strongly convex. (5) Cu_2 (1st A in Forbes' nomenclature) is a notoriously weak vein in all insects. It lies in the bottom of the cubital furrow and disappears often in several orders, including many Coleoptera. (6) The remaining veins of the wing are all concave, all lie distinctly behind the cubital furrow, and all are associated with the third axillary; conditions which seem to mark them as the second and following anals. Unless 1st A forms a branch of the three-branched vein, 1st A is unaccounted for, and the vein here called 1st A does not disappear often. At this point one is forced to assume that 1st A crossed the cubital furrow and united basally with Cu_1, probably after the atrophy of Cu_2.

The second branch of the three-branched vein is distinctly convex, and lies well away from the cubital furrow. Hence it seems unlikely that it is Cu_2, and it must, of necessity, be a second branch of Cu_1—Cu_{1b}.

Interpretation of the remainder of the wing is not difficult. The jugal fold is well defined, and between it and the cubital furrow are two concave veins. There is no reason to doubt their homology with the veins occupying the same region in wings of other Coleoptera. The vein here called 2nd A is the 3rd A of Forbes; normally two-branched, but in this wing reduced to a single vein. 3rd A in fig. 2a may then be considered Forbes' 4th A. The above interpretation is almost identical to that of Redtenbacher, who came to it without the use of basal sclerites in 1896.

The features of such a venation seem to point to an exceedingly remote ancestry for this genus. Forbes notes, and it has been observed by others, that there is no vein in the Coleoptera which could be considered "Cu_2" (Cu_{1b} in the terminology used here). If this interpretation is correct, Cu_{1b} has been retained in *Atractocerus*.

The lack of crossveins (*Atractocerus* has only one) also seems to indicate considerable divergence. One would expect the loss of the radial crossvein with the loss of the radial sector, but the loss of the *m-cu* crossveins and *cu-a* is less easy to explain if *Atractocerus* is to be considered close to other forms.

In a recent (1952) paper on the affinities of *Telegeusis*, H. S. Barber stresses the close relationship of that genus to *Atractocerus*. The females of *Telegeusis* are unknown; the wing of *T. debilis* is illustrated in figure 4. To quote from Barber: "The modified alar venation of *Atractocerus* and *Telegeusis* appear comparable and derived from the primitive venation of *Lymexylon*, the differences between the first two being such as are necessary for the swift and powerful flight of *Atractocerus* in contrast with that of the feeble Sonoran form." The venation of *Telegeusis* could indeed have been derived as Barber suggests. However, *Atractocerus* must have been derived not from *Melittomma* (*Lymexylon*) which has lost Cu_{1b} (fig. 5), but from some ancestor of *Melittomma* which did possess this vein. The wing of *Telegeusis* is a typical Polyphagous type, with somewhat reduced venation and quite orthodox folding.

As has been mentioned, the wing of *Atractocerus* lacks any sign of transverse folding. This fact in itself is somewhat remarkable. Wings which have secondarily lost their folding, such as *Necydalis*, still retain the interrupted venation of a previously-folded wing. The veins of *Atractocerus*, excepting the *r-m* crossvein which is crossed by a longitudinal fold, show no weakening whatever. They are spaced in such a way that folding of the tip of the wing, even in the manner of the Serricornia, is impossible. This evidence alone seems sufficient to suggest that the ancestors of this genus never did fold their wings as did practically all other beetles.

To summarize, the evidence drawn from the wings rests on: (1) the retention of Cu_{1b}, (2) the lack of crossveins in the Cubital and Anal fields, (3) the absence of interruptions in the tips of the longitudinal veins, and (4) the absence of transverse folding.

The Female Genitalia

In 1927 Tanner reviewed in some detail the anatomy of the female genitalia in 66 families of beetles. He notes a difference between the "compact" Adephagous type and the "elongate" Polyhagous form. Tanner's conclusions on phylogeny, insofar as they are pertinent to the present problem, are summarized briefly below:

1. The coleopterous female genitalia consist of parts which may be homologized with little difficulty within the order.

2. The Caraboidea (i.e. the Adephaga exclusive of the Gyrinidae) are "a very primitive group," since there may be found in the Caraboidea all the parts present in any Polyphagous species.

3. The Caraboid genitalia are compact and complex, with broad, sclerotized coxites, sternites and valvifers, while the Polyphagous families are characterized by their narrow, comparatively membraneous genitalia with all sclerites reduced.

No evidence is offered, nor does Tanner claim, that his series Caraboidea were themselves ancestral to the Polyphaga. However, the implication is made that *because* all parts of the genitalia are present and recognizable in the Caraboid type the ancestral form must have been of that type. The figures of Caraboid genitalia given by Tanner show far greater complexity than do those of the more simple, elongate Polyphaga; and Tanner notes this, apparently without being impressed with the possibility of another point of view.

It is suggested that if the earliest female Coleoptera possessed genitalia with all the structures of Tanner's Caraboid type, but possessed them in a simple, unmodified condition, then that form could have diverged on the one hand to give rise to the complex, compact type now seen in the Adephaga, and on the other hand to produce the elongate form with its reduced sclerotization which is prevalent among the Polyphaga.

Such an ancestral form may have resembled *Brathinus* (fig. 6), which is redrawn from Tanner and appears to represent a very simple type. Genitalia of *Atractocerus* were not illustrated by Tanner, but he does figure those of *Hylecoetus*, a primitive Polyphagous type, redrawn in fig. 7. The genitalia of *A. brasiliensis* (fig. 8), resemble those of *Hylecoetus* more closely than they do those of any other species figured by Tanner. Differences between the two are readily apparent, but most

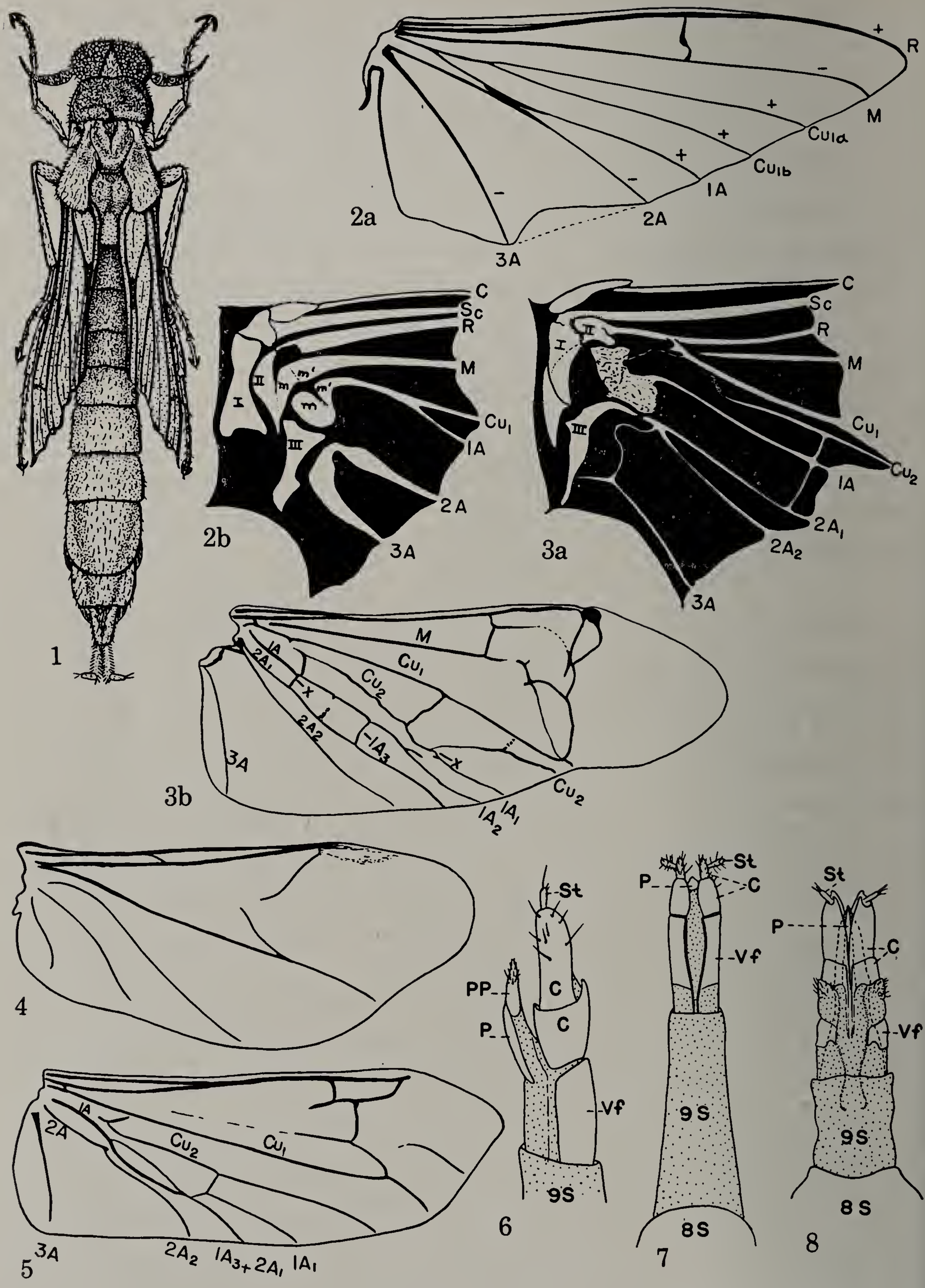

FIG. 1. *Atractocerus* sp. Female. FIG. 2a. *Atractocerus* sp. Wing. FIG. 2b. *Atractocerus* sp. Wingbase I, II, III, Axillary sclerites; m, m′, median plate. FIG. 3a. *Cupes concolor*. Wing base. FIG. 3b. *Cupes concolor*. Wing. Abbreviations as in 2b. FIG. 4. *Teleguesis debilis*. Wing. FIG. 5. *Melittomma sericeum*. Wing. FIG. 6. *Brathinus*

significant is the retention of the elongate, sclerotized proctiger by *Atractocerus.* The proctiger of *Hylecoetus* is reduced to a small button. Valvifers are large in *Hylecoetus* and *Brathinus;* small in *Atractocerus.* It seems reasonable to suggest that both *Atractocerus* and *Hylecoetus* must have come from an ancestor in which both proctiger and valvifers were well-developed. *Atractocerus* then apparently reduced the valvifers and retained unchanged the elongate proctiger, which *Hylecoetus* retained elongate valvifers and reduced the proctiger. On the basis of this character the two forms appear to be not closely related.

The Male Genitalia

Little can be deduced from the male genitalia that assists in the present problem. Sharp and Muir (1912) note that the two species of *Atractocerus* they studied "differ from one another and do not approach to any of the trilobe forms." In this they are certainly quite correct. There seem to be no significant similarities between the genus in question and its putative relatives when the male genitalia are considered.

The Maxillae

One of the features which appears to unite *Atractocerus, Melittomma, Hylecoetus,* and *Telegeusis* in a single superfamily is the fact that each genus possesses highly modified, flabellate maxillae. Maxillae of the first three of the above genera are illustrated in figures 9-11 respectively. Their similarity lies in the Y-shaped structure which arises from the third segment of the palpus. The maxilla of *Telegeusis* does not show the thumblike process common to the other three. *Hylecoetus* and *Melittomma* have four distinct palpal segments; *Atractocerus* three indistinct ones. Of the three genera, *Atractocerus* shows the greatest divergence from what might be called an "orthodox" maxilla. This is not inconsistent with the idea that it departed from the main line of beetle ancestry at an earlier date than the other two genera. Under this view, the similarity of the maxillary process is a parallelism.

Larvae

The larva of *Atractocerus* appears neither to support nor refute the hypothesis here presented. It is a woodborer, with the general features of the Polyphaga, and while it is readily separable from the other genera under consideration, there seem to be few characters of phylogenetic significance. Barber notes similarities between *Atractocerus* and

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sp. Female genitalia, redrawn from Tanner. C, coxite; P, proctiger; PP, paraproct; S, sternite; St, stylus; Vf, valvifer. Fig. 7. *Hylecoetus* sp. Female genitalia, redrawn from Tanner. Abbreviations as in 6. Fig. 8. *Atractocerus brasiliensis.* Female genitalia. Abbreviations as in 6.

Lymexylon, but it is difficult to say whether they indicate a truly close relationship or parallelism in response to the lignivorous habit.

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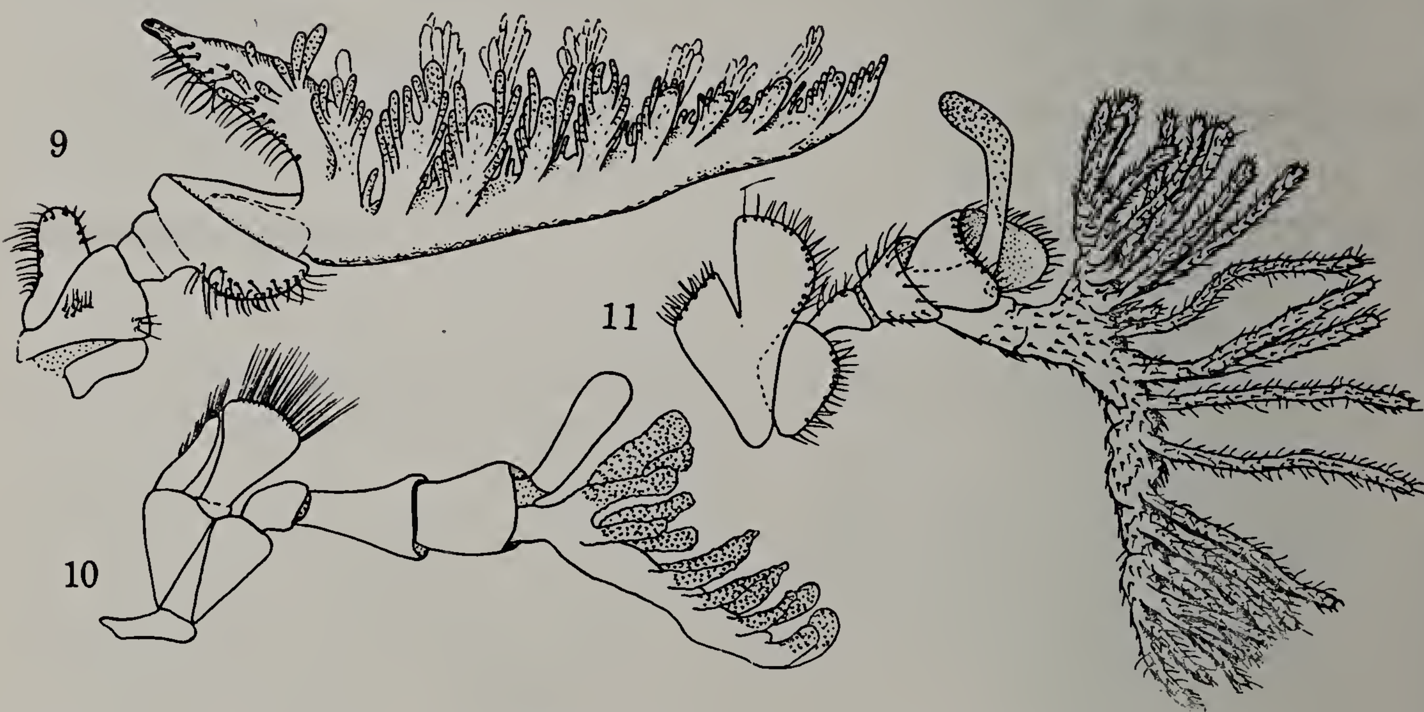

FIG. 9. *Atractocerus* sp. Maxilla. FIG. 10. *Melittomma sericeum.* Maxilla. FIG. 11. *Hylecoetus* sp. Maxilla.

The larval leg has a single claw. The megalopterous ancestor of the Coleoptera very probably had a two-clawed larval leg, as most of the Adephaga larvae do today. The Polyphaga as a group have only one claw, but before *Atractocerus* is placed with the other polyphagous families on this evidence alone, it should be remembered that the tendency to reduce two larval claws to one is not unknown in other holometabolous groups, notably the Hymenoptera. Such reduction has occurred at least once in the Hymenoptera, and at least once in the Polyphaga. It is not beyond the bounds of possibility that it has taken place independently in this genus.

CONCLUSIONS

On the evidence of wing folding, venation, and genitalia the point of view appears tenable that the ancestor of the genus *Atractocerus* diverged from that of the remainder of the Coleoptera after the development of elytra and before the formation of the usually accepted suborders. In doing so it (1) retained certain venational features, (2) failed to develop wing folding, (3) acquired individual and independent structures of the genitalia, and (4) developed some features of the maxilla and larva in parallel with those of its closest relatives among the primitive Polyphaga. The phylogeny here expressed is diagrammed in figure 12.

The designation of the species of this genus as the family *Atractoceridae,* as has been done in the past, appears quite justifiable. Their relationship to the suborders Adephaga, Archostemata, Polyphaga, and Strepsiptera seems to be best shown in designating the genus and family as the new suborder APLICALAE, or Coleoptera in which the wings have remained primitively without transverse folding, and possess the other features already discussed.

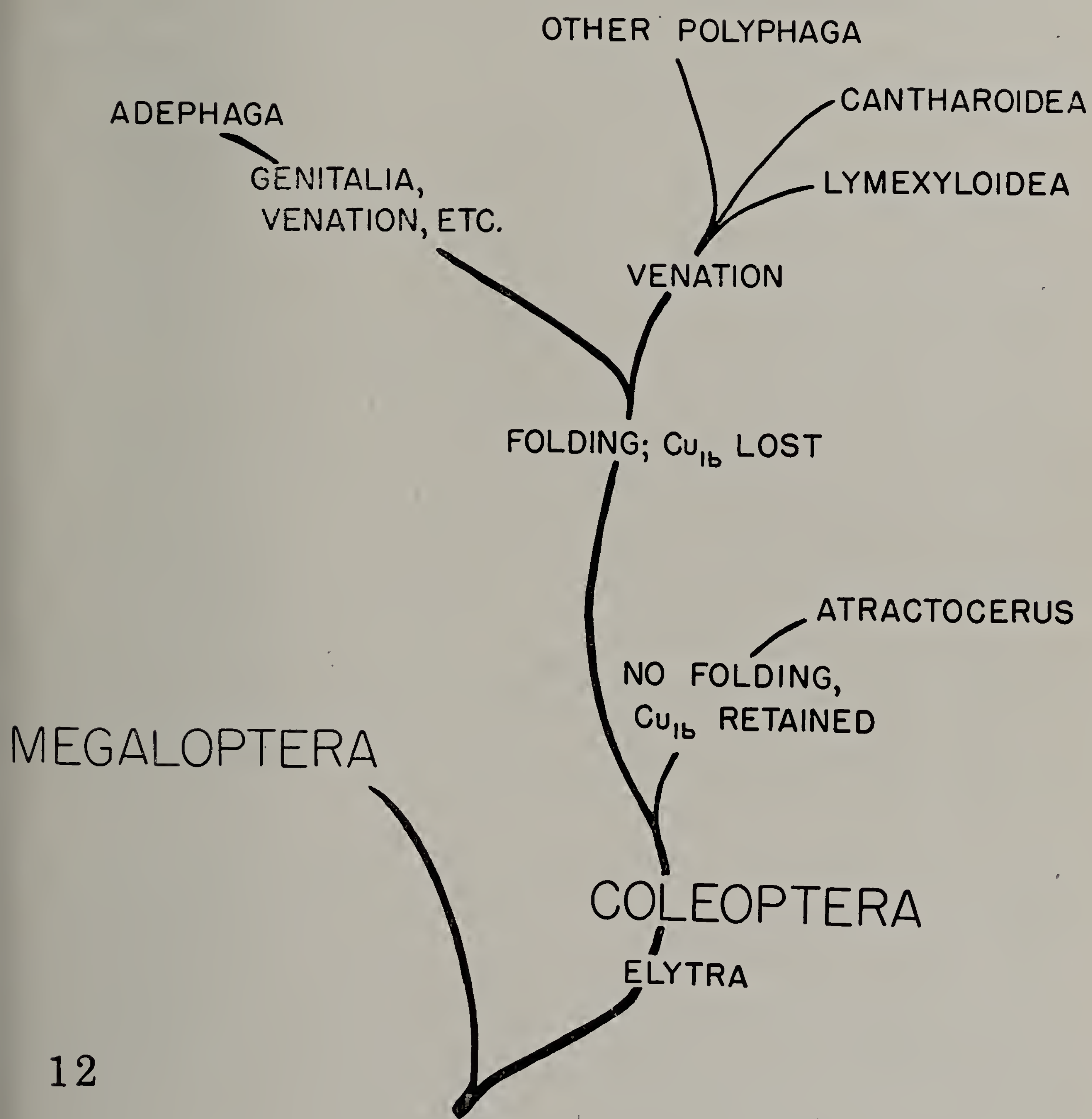

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Fig. 12. Relationship of *Atractocerus* to the Megaloptera-Coleoptera Stem and to the major divisions of the Coleoptera.

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UNUSUAL ABUNDANCE OF *SANDALUS* IN SOUTHERN INDIANA

In September, 1954, a *Sandalus,* tentatively determined as *niger* Knoch, was found in some numbers in the dry woodlands in the Scott's Pond area near Bloomington, Monroe County, Indiana. Males were observed on the morning of September 25 flying at heights of 4 to 15 feet, but no females were taken in flight. The buzzing of several males attracted our attention to a large female together with two males resting about 12 feet above the ground, on the trunk of a small hickory. Other males were seen to veer in flight and approach this group. Some came to rest and then took off so that the males resting on the trunk seemed to be changing constantly. By standing beneath the tree it was possible to net the males as they flew to and from the trunk, and nearly a dozen were collected in less than an hour. A smaller female with a smaller coterie of males was found on a tree nearby. Both females and most of the males were very dark; only one male was light brown.

The area in which these beetles were found has been rather thoroughly explored in connection with ecological studies of other insects every year since 1950, but no specimens of *Sandalus* have been collected or observed before. It thus seems possible that the unusual abundance in 1954 was connected with the emergence of Brood X of the Periodical Cicada (*Magicicada septendecim*) which occurred in the general area in 1953.—FRANK N. YOUNG, *Indiana University*

News

DR. TAKEHIKO NAHANE is now editor of the Japanese journal of entomology AKITSU. Volume 4, no. 4 is now in press. Volumes 1-3 were published by the Takeuchi Entomological Laboratory, Kyoto, 1937-1943 and all papers were written in Japanese. The present volume is published by the Kyoto Entomological Society and includes paper written in English. Volume 4 contains 116 pages in total, of which 45 pages are written in English containing descriptions of new forms of Cerambycidae, Erotylidae, Mordellidae, Nitidulidae, Elateridae, Niponiidae, Carabidae, Dytiscidae, Trogidae, Ciidae, Lycidae, as well as descriptions of a few orders other than Coleoptera.—R. H. ARNETT, JR.